SUBTERRANEAN ORGANS OF BOG PLANTS

CONTRIBUTIONS FROM THE HULL BOTANICAL LABORATORY 288

FRED W. EMERSON

(WITH ELEVEN FIGURES)

Introduction

There has been much research on the subterranean organs of plants from many standpoints. The analytical study of these organs as they grow in nature, however, has chiefly been limited to comparatively recent work. In 1899 and 1900 HITCHCOCK (4) published results of work done on the Kansas flora, in which were brief descriptions of the underground parts of a considerable number of native plants, with notes on habitat and length of life. CANNON (1, 2) in 1911 and 1913 added greatly to our knowledge of the behavior of roots in the soil, showing that some of the current ideas have at best been incomplete, and that in the desert there is a wide variation in root behavior. More recently a number of papers have appeared adding information about the root and rhizome systems in a variety of habitats. Among them are papers by HAYDEN (3), MARKLE (6), PULLING (7), and WEAVER (9, 10).

The present paper deals with work carried on in an attempt to discover, first, the exact behavior of the underground parts of plants growing in peat bogs, and to some extent to compare these organs with those of the same species growing in mineral soil; and second, to determine as far as possible the factors involved in any peculiarities in behavior noticed.

While there are many references in the literature to the comparatively shallow roots in swamp lands, it seems that no one has gone into detail in determining just how shallow the roots and rhizomes are, nor with a few exceptions have the biological relationships of these parts been analyzed. YAPP (12) has described some of the relationships of roots and rhizomes in the fen, and SHERFF (8), in his analysis of the subterranean organs in Skokie Marsh, has gone into somewhat greater detail. In neither of these papers, however, is work reported on the typical peat bog plants.

The main station for this study was Cedar Lake, at Lake Villa, Lake County, Illinois. Supplementary work was carried on in bogs at Miller and Hillside, Indiana, and in a fen at Wolf Lake, Indiana. Cedar Lake is located about five miles south from the Wisconsin line and twenty-two miles west from Lake Michigan. It is situated in the Valparaiso morainic system (5) in a considerable depression in the drift. The western border of the lake is deep and is covered by a floating mat of fibrous peat, while the north and east sides are shallow, and the vegetation passes from the usual hydrophytic forms in the water to shrubs, sedges, and grasses on the shores. This gives opportunity for comparing certain species as they grow in both peat and mineral soils, but with other conditions as nearly the same as is possible to find them in nature. The bog under consideration is of crescent form, fringing the west end of Cedar Lake, and is about 200 m. in width at its widest part. It is composed of a floating mat of peat that is only slightly decomposed, except where it comes in contact with the clay basin at its landward margin. Here it has decayed, forming a hummocky black soil. Judging from its small size, the fact that it has made but a beginning in covering the lake although it is evidently making measurable progress, and the absence of all trees with the exception of a few young tamaracks, it seems evident that this bog is geologically very young. When compared with the vegetation of other bogs of the region, the plant life of this bog is obviously in the very early stages of plant successions, and it is inconceivable that it dates back to glacial times. Thus the supposition that all bogs are relicts from the glacial period seems less plausible.

Field study

In order to determine the exact form and physical relationships of the roots and rhizomes of bog plants, the preliminary work undertaken was the mapping of these parts *in situ*. The organs in question, some of which were very tender, were followed with the finger tips and then laid bare by the removal of all the material above them. Careful measurements were taken and the maps were made to scale on coordinate ruled paper (figs. 1, 3, 4, 6). In this work it soon became evident that, with the exception of a few species, living plant parts were very rare below a certain comparatively slight depth, and that each species had its own characteristic range of depths. In most cases the roots and rhizomes maintained almost the same level throughout their length. Hence in mapping it was necessary to show only the horizontal arrangement of the organs in question, stating the depth from the surface or the relation to the water table. Since the mat is held up by its own buoyancy, the surface remained at practically the same level

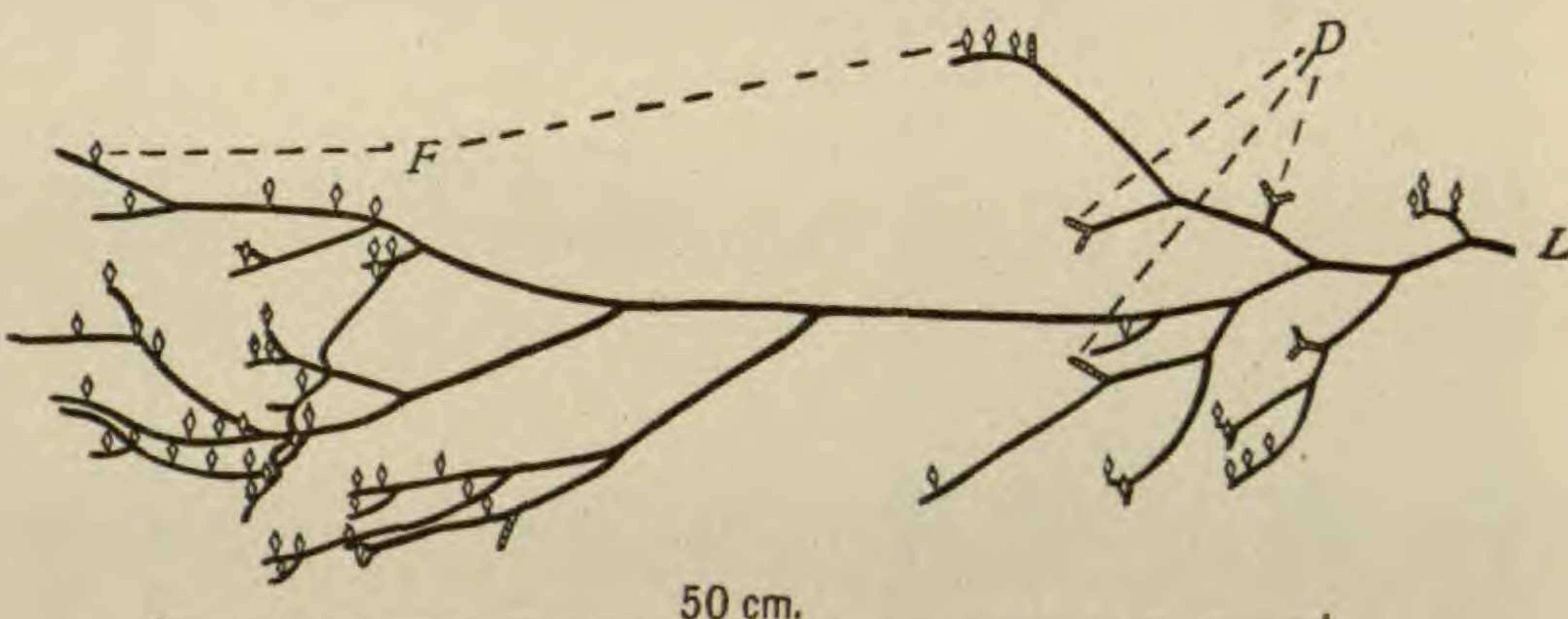


FIG. 1.—*Aspidium Thelypteris*, map of rhizome system: *L*, living attachment to older part of system; *D*, dead tips of rhizomes; *F*, foliage leaves; solid black lines, living rhizomes; note numerous dead rhizome tips, represented by cross lines on white ground, in older parts; dying behind the dichotomous branches leaving them independent is a very common means of multiplication in this fern; depth 4–6 cm.

throughout its extent and throughout the growing season. This distance from soil surface to water table was approximately 6 cm. As may be noted in the maps, the underground parts of bog plants are remarkably straight when compared with those of upland plants. Doubtless this is largely because of the lack of mechanical interference to the growing parts by the spongy peat. The more important species represented in this bog are as follows.

Sphagnum.—This plant grows abundantly over most of the floating mat, especially toward the lakeward margin. It was found to be propagating vegetatively by growing above and dying below. No other means of propagation was found. It appeared to remain alive to a depth of 3–4 cm.

Aspidium Thelypteris.—This species was studied in both bog and swampy mineral soil. The rhizomes were found to be always horizontal. The depth was 2–6 cm. in bog soil, and 1–6 cm. in mineral soil. In no case were living parts found below water. The roots were almost horizontal when near the water table, but nearly vertical and going down to 15–17 cm. deep in a substratum that was only moist. No difference of any sort was apparent in peat and mineral soil. Fig. 1, which is a map of most of the rhizome

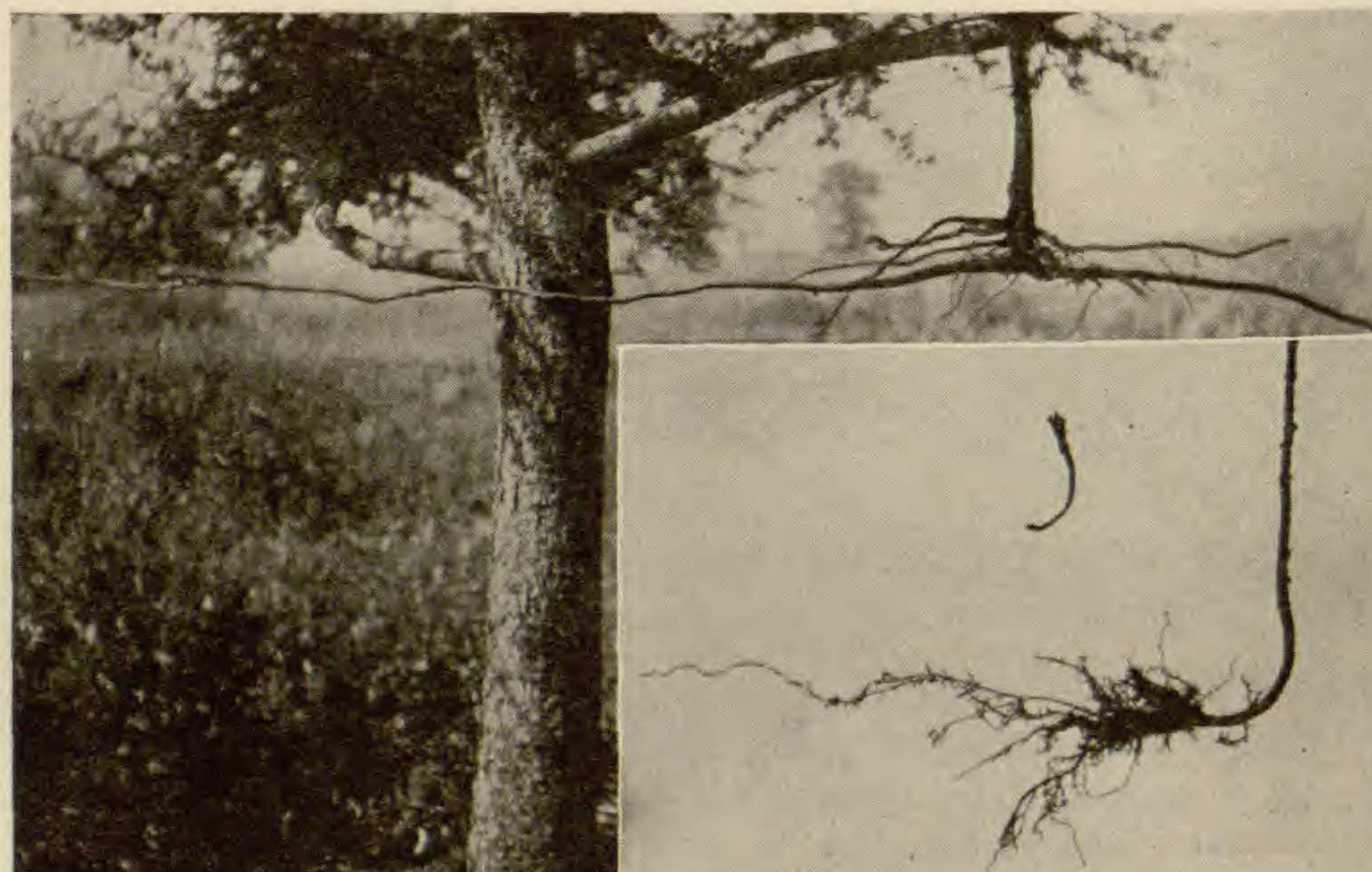


FIG. 2.—*Larix laricina* with roots showing horizontal position; inset, young seedling and plant three or four years old showing tap root becoming horizontal; maximum depth 6 cm.

system of one plant, shows that in the older parts there are numerous dead rhizome tips and few leaves, while in the younger parts the plant is vegetating very freely. The older parts were much discolored and too brittle to trace farther than is shown in the map.

Larix laricina (fig. 2).—The larch had no tap root, all the roots being horizontal and above the water level, except where the weight of the tree forced them deeper into the peat. All living roots were 6 cm. or less in depth. There were only a few dozen comparatively young larches in the bog in question. No other tree species was found.

Typha latifolia.—The rhizomes of this species assume about the same depth in mineral or peat soil. Those measured varied from 15 to 30 cm. deep in peat, and from 12 to 25 cm. deep in mineral soil. The roots extended diagonally or vertically downward. The deepest extended far below water in both types of soil. A few of the vertical roots were found exceeding 60 cm. in depth. On account of the turbid water they could not well be followed to a greater depth.

Sagittaria latifolia.—This species is not very common in the bog, but is included because it also grows outside of the bog and affords opportunity for comparison in the two habitats. While there is considerable variation in the depth of various parts of a given

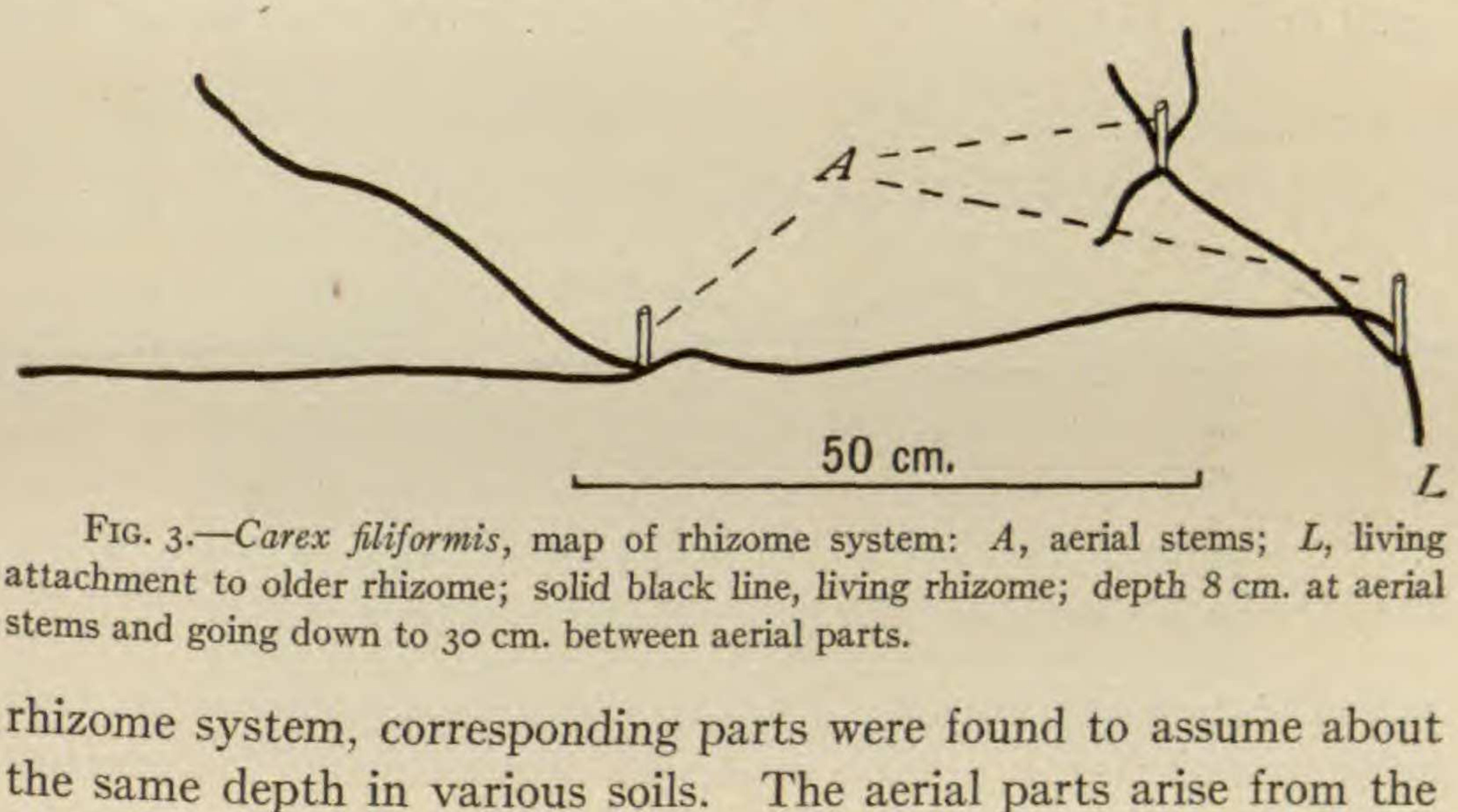


FIG. 3.—*Carex filiformis*, map of rhizome system: *A*, aerial stems; *L*, living attachment to older rhizome; solid black line, living rhizome; depth 8 cm. at aerial stems and going down to 30 cm. between aerial parts.

rhizome system, corresponding parts were found to assume about the same depth in various soils. The aerial parts arise from the rhizome at about 4–6 cm. deep, while at other places the rhizome gradually descends to depths of 10 cm. or more. The root behavior is almost identical with that of *Typha latifolia.*

Scirpus validus.—The rhizomes assumed a depth of 12–15 cm. in all soils where the species was found. A few of the roots extended downward to a depth of 30–40 cm. Nearly all of the roots were vertical, hence the entire subterranean system was below water. This bulrush was fairly common along the lakeward margin of the bog as well as in fens.

Carex filiformis.—This sedge was found in the bog only. Its roots and rhizomes varied in depth from 5 to 30 cm. The roots were approximately horizontal (fig. 3).

Pogonia ophioglossoides (fig. 4).—While this orchid plays no pronounced part in the building of the bog, it is included on account of the peculiar character of its subterranean system. This is made up of a simple but comparatively extensive root system from which the aerial parts grow. This plant has no rhizome, although the root behaves in a manner similar to a rhizome and forms an effective means of vegetative propagation. Branches proper are lacking in the roots, but one or two new roots are likely to arise adventitiously from the base of each aerial shoot. This entire root is 5–6 cm. deep, which is just at the surface of the water in the bogs studied.

Calopogon pulchellus.—In contrast with *Pogonia*, this orchid has very little root system, the chief underground part being a small bulb. The bud of this bulb frequently divides, making two

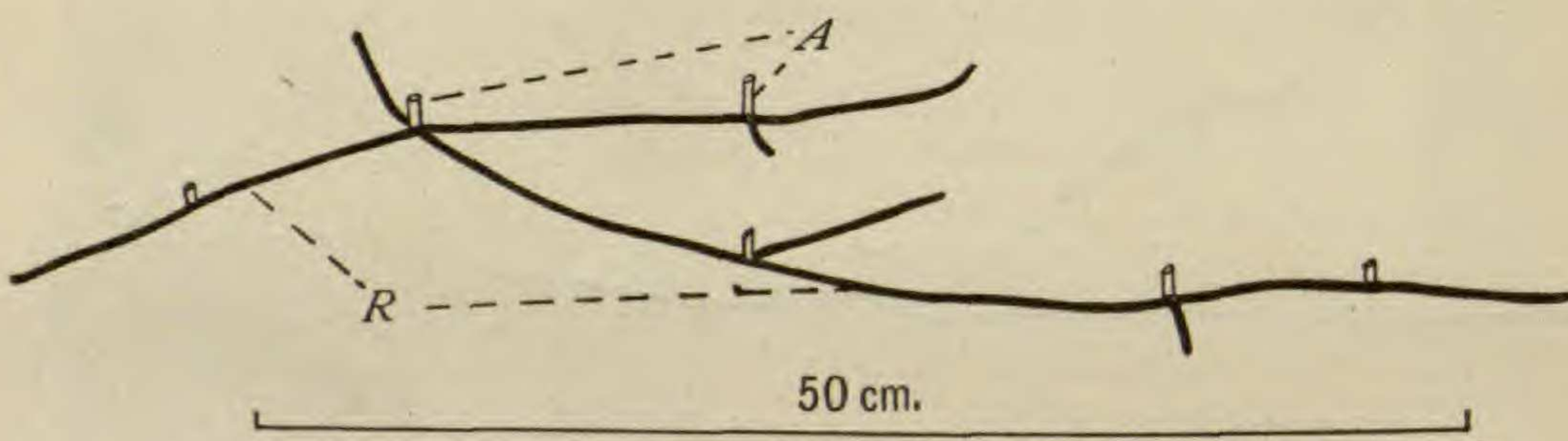


FIG. 4.—*Pogonia ophioglossoides*, map of root system: *A*, aerial stems; *R*, root; plant propagated by roots instead of rhizomes as usual in most bog plants; depth 6 cm.

new plants, which, however, are likely to remain attached to each other, hence this is a poor means of disseminating the species. The few simple roots and the bulb structures were found to be dead at about 6 cm. deep, hence no living parts were found below the water.

Betula pumila.—The dwarf birch grows obliquely or vertically upward, putting out roots at various levels in the peat. These roots assume an approximately horizontal position. They were found at various levels from 6 to 18 cm. deep.

Sarracenia purpurea (fig. 5).—This species has a vertical stem, and distorted, usually vertical adventitious roots growing out wherever the stem is covered with peat. All structures die at the water surface.

Drosera rotundifolia.—This plant behaves similarly to *Sarracenia*, except that its living parts do not extend deeper than 2 or

3 cm., and there are not more than three or four feeble, unbranched roots living at any time. Although a comparatively small plant, it appears to be able to grow upward rapidly enough to keep from being covered by the *Sphagnum* in which it often grows.

Lathyrus palustris (fig. 6).—The rhizomes and roots are horizontal in this species, and were not found living below water. The rhizomes were mostly about 5 cm. deep. The roots were few in number, short, and only slightly branched. Those around the aerial stems had numerous large tubercles containing bacteria.

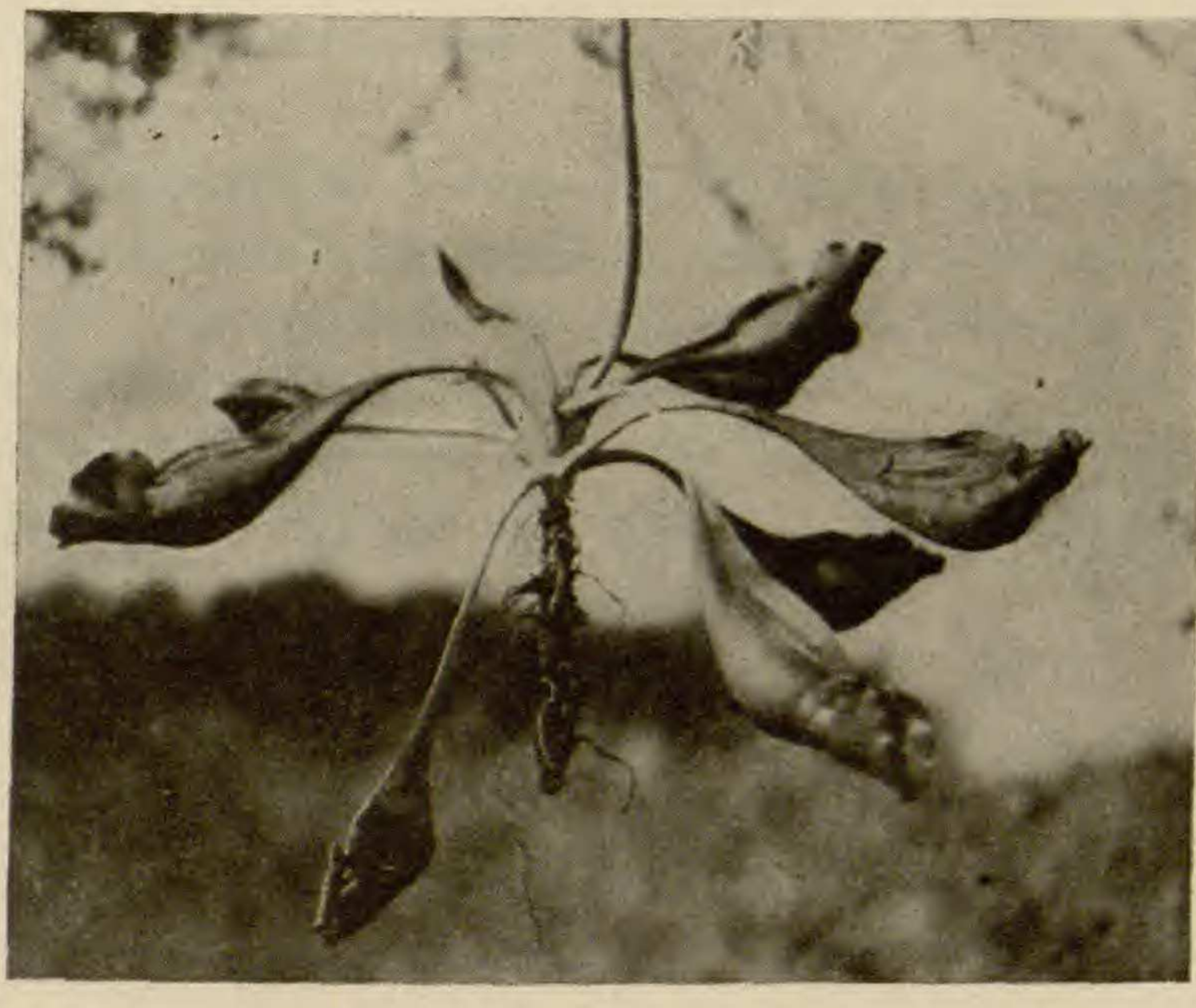


FIG. 5.—*Sarracenia purpurea*, entire root system; stem and roots dead below depth of 6 cm.; roots in normal position.

Decodon verticillatus.—This species is the most prominent pioneer extending the floating mat out over the lake. Wherever the stems come in contact with water, large amounts of cortical aerenchyma form and numerous adventitious roots grow down. Considerable quantities of peat cling to this mass of stems and roots, and thus a floating substratum is formed on which other plants soon begin to grow. Among the most common of these are *Sphagnum*, *Aspidium*, and *Scirpus*. The greatest depth to which the roots of *Decodon* descend in the water was not determined accurately, but it was found that they attain at least a depth of more than 40 cm.

Vaccinium macrocarpon.—Where the prostrate stems of the cranberry come in contact with the moist peat, numerous short adventitious roots appear growing diagonally downward or almost horizontal. As the peat forms above and the roots and stems are weighed down to the water level, they die at the surface of the water. This species, growing with *Aspidium Thelypteris*, forms a tough woody network over a considerable part of this bog.

Menyanthes trifoliata.—The rhizome of this plant assumes an approximately horizontal position from 3 to 9 cm. deep, while the roots may either be horizontal or vertical. The roots were found as much as 12 cm. deep. They were few in number and comparatively short but much branched.

Eupatorium perfoliatum.—The base of the stem of this species assumes an approximately horizontal position near the soil surface

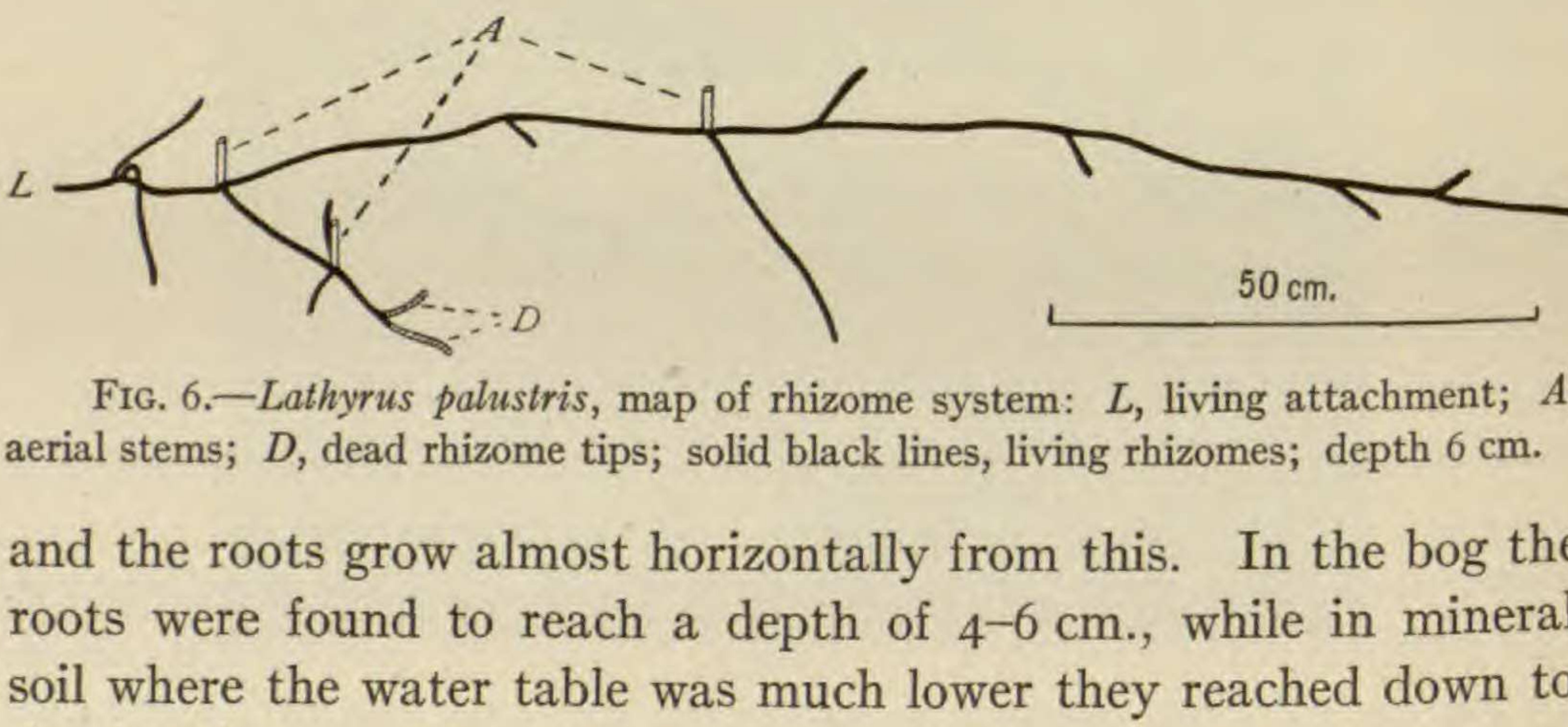


FIG. 6.—*Lathyrus palustris*, map of rhizome system: *L*, living attachment; *A*, aerial stems; *D*, dead rhizome tips; solid black lines, living rhizomes; depth 6 cm.

and the roots grow almost horizontally from this. In the bog the roots were found to reach a depth of 4–6 cm., while in mineral soil where the water table was much lower they reached down to depths of 5–10 cm.

It should be noted that a very high percentage of all the living plant tissue in the bogs studied is above the water level. The part above water usually consists of a mat about 6 cm. thick, made of a coarse feltlike tangle of living roots and rhizomes largely of *Aspidium*, *Carex*, *Vaccinium*, and *Menyanthes*, and often a dense growth of *Sphagnum*. It is difficult to penetrate this tough mat, while just below the water level a sharp contrast appears. Here a fibrous, light brown peat is found in which the dead parts of these same species can often be recognized to considerable depths. Almost the only living parts encountered are occasional roots or rhizomes of *Typha*, *Sagittaria*, *Scirpus*, or *Eriophorum*.

MARKLE (6) working in New Mexico, and WEAVER (9, 10) in the prairies, have noted that two dominant species in an association are not likely to have their roots so placed as to have any marked subterranean competition. This is obviously not the case in the main parts of this bog flora, where two codominants, *Vaccinium macrocarpon* and *Aspidium Thelypteris*, have practically the same level, and together dominate the greater area of the bog. Neither of these two dominant species seems to be overcoming the other. Mingled with these are a number of less important species also at the same level. On the other hand, the deep-rooted forms in which there is no competition are in no case crowding out the shallow rooted species.

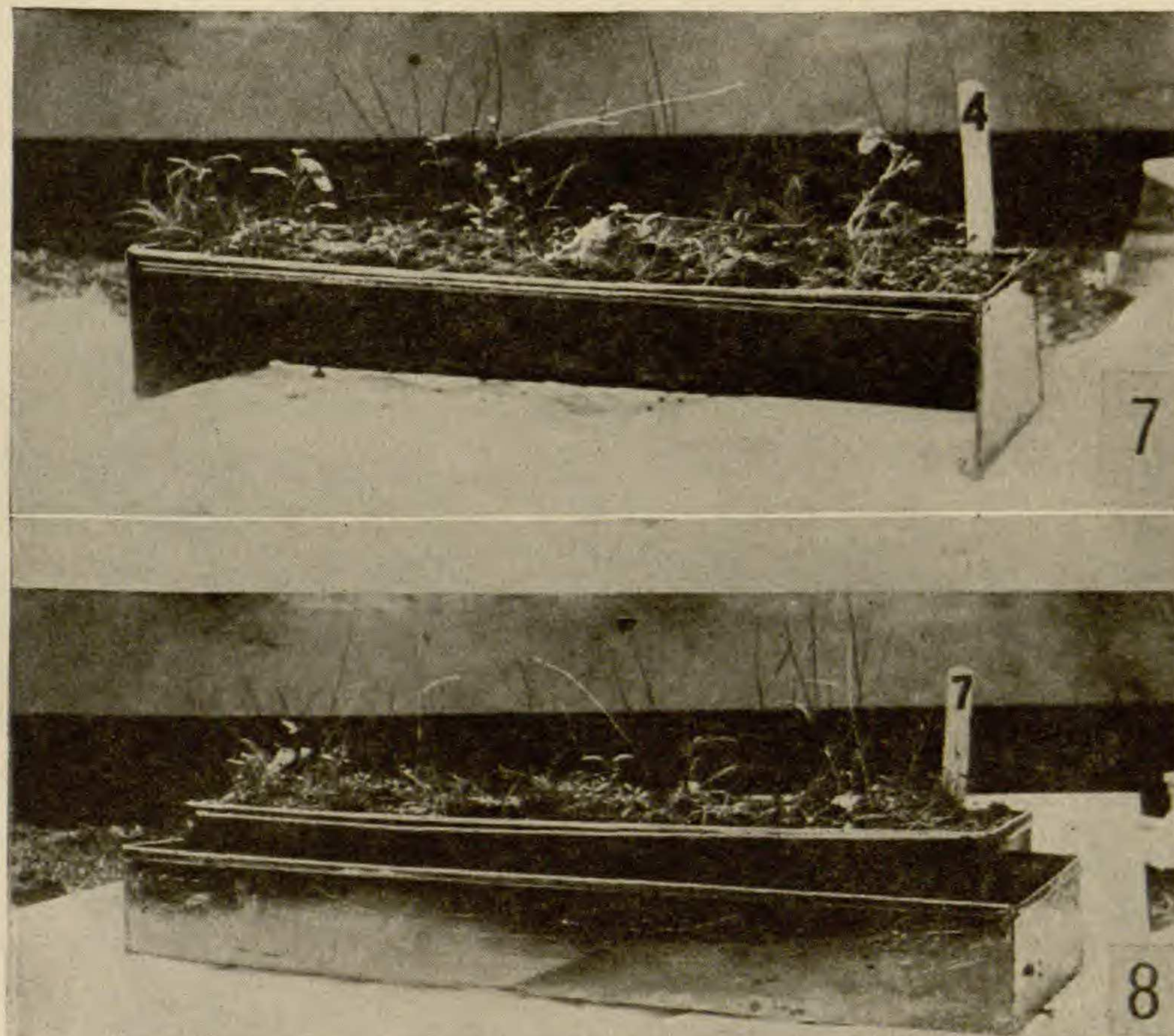
Aerenchyma is very common both above and below the water table. Roots and rhizomes which grow below water are all very rich in air tissue, with the exceptions of *Betula pumila* and *Salix* spp. In these species no aerenchyma was found in any of their parts, nor, with the exception of *Decodon verticillatus*, was it found in any woody perennial examined. In most cases herbaceous species have a great deal of aerenchyma.

Tests for H ion concentration in the soils were made by means of the colorometric indicators made by the La Motte Chemical Products Company. The records were made in terms of specific reaction (11). The tests were made in the white porcelain "spot plates," such as are commonly used in the chemical laboratory. By means of pipettes the water to be tested was drawn off from the absorbing parts of the roots. In all cases fruiting or flowering plants were used. Both pipettes and spot plate were thoroughly rinsed in the water to be tested before beginning each test. A series of samples was taken across the bog from the lakeward margin toward the landward side. The water of the lake was uniformly 30 alkaline. The reaction on the floating mat gradually changed from alkaline to neutral, and finally reached 10 acid, 2 or 3 m. from the lakeward margin. This reaction was uniform across the entire mat until the decaying peat was reached on the landward side. Here the acidity decreased until it reached neutrality at a point where the mat was so decomposed that it would no longer bear the weight. It was not possible in any case to discover a difference in reaction in the water drawn from the immediate surface of the roots and that taken from the peat near by. Hence it seems that all roots in a given area are subject to approximately the same soil reaction. Members of a given species, however, often showed considerable latitude in tolerance to soil reaction. The widest variation found was that of *Larix laricina*. At Mineral Spring, Indiana, in a very old bog in which the peat has become considerably decayed, the reaction about its rootlets was 10 alkaline; at Hillside, Indiana, in a mature bog of fibrous peat, 300–1000 acid; and in the comparatively young mat at Cedar Lake, 10 acid. No marked differences could be seen in subterranean systems of members of the same species growing in peat and mineral soils, or in various natural concentrations of H and OH ions.

Other species which showed a narrower range of tolerance to reaction follow, with the extremes of reaction found in each. Water squeezed from *Sphagnum* had a specific acidity of 100 to 1000; *Aspidium Thelypteris*, *Scirpus validus*, and *Betula pumila* all varied from 10 alkaline to 10 acid; *Sarracenia purpurea*, *Drosera rotundifolia*, and *Vaccinium macrocarpon* varied from neutral to 300 acid. The peat about the roots of *Decodon verticillatus* at the margin of the mat was approximately neutral, while the lake water into which this species was migrating was 30 alkaline.

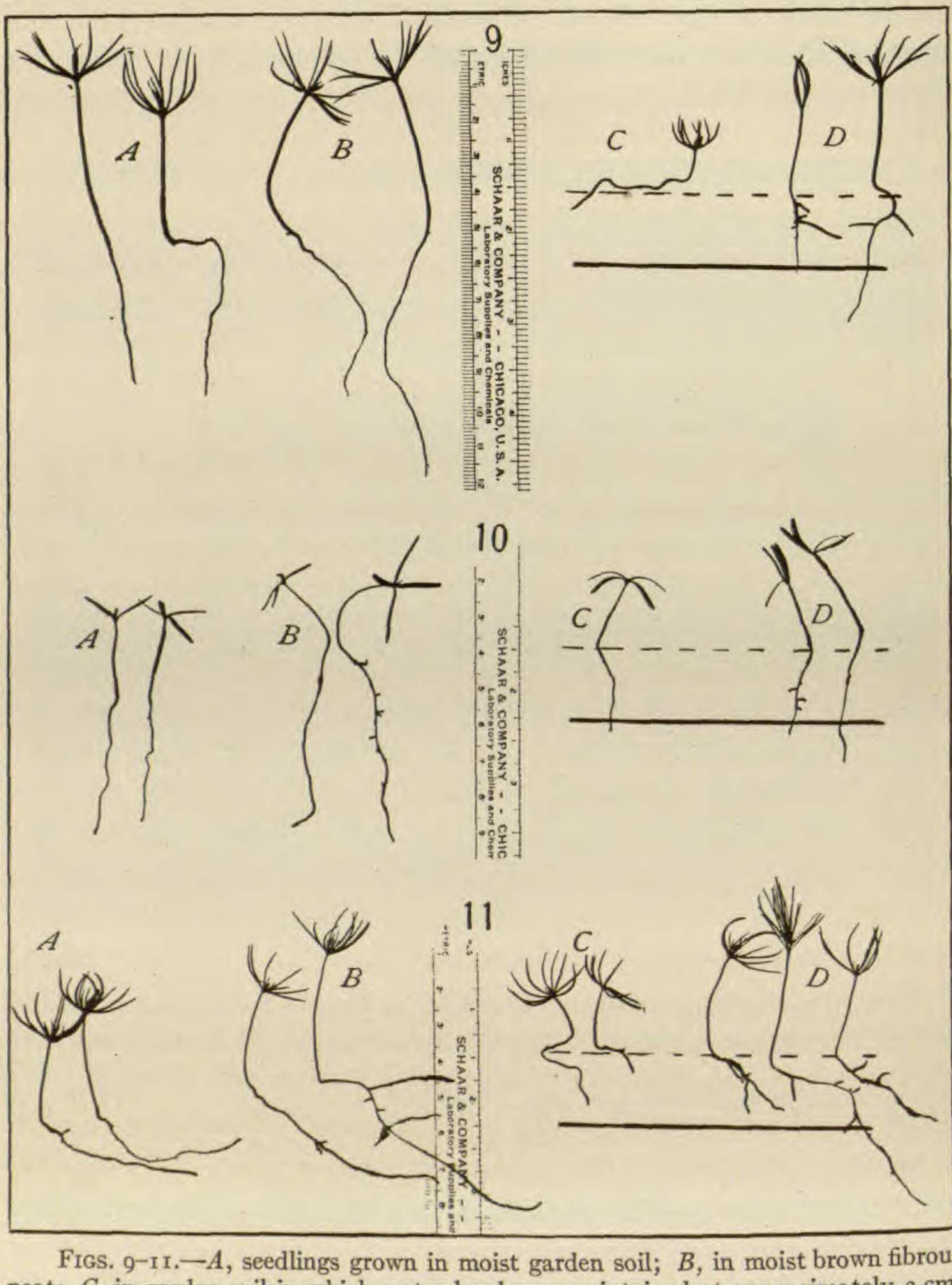
Experimentation

In order to determine the factors involved in the horizontal placing of roots in bogs, the following experiment was carried out. Galvanized iron boxes, 10 cm. × 15 cm. × 55 cm., were made with the bottom and one side replaced by a diagonal pane of glass. This glass was covered on the outside by a piece of galvanized iron which could readily be removed, making it easy to make observations of the roots, but at the same time keeping them protected from the light except during examination. In certain parts of this experiment, as indicated later, a fixed water table was maintained by keeping the boxes in pans of water of proper depth (figs. 7, 8). All metal surfaces were given two coats of Acme asphalt varnish. Various germinating seeds were planted in these boxes. The most significant results are shown in figs. 9–11. Distilled water was used throughout the experiment for watering the seedlings and maintaining the water level. This distilled water had a reaction of approximately 1 (neutral), although in some cases it showed a slight trace of acidity from carbonic acid. All the peat maintained



FIGS. 7, 8.—Growing boxes used in experimental work: fig. 7, growing box with diagonal glass side facing camera (removable sheet iron false side is in place covering glass); fig. 8, growing box similar to that in fig. 7 placed in pan containing water, thus maintaining fixed water level in growing box.

a specific acidity of 3 throughout the experiment. The garden soils varied from specific reaction 1 to specific alkalinity 10. This last reaction was reached near the end of the experiment in the wet garden soil. The experiment was carried on for about two months during February, March, and April, 1921, in the cool room of the greenhouse. At the end of this period the plants were removed from the soil and characteristic specimens, showing as far as possible the extremes of size and form, were photographed.



FIGS. 9–11.—*A*, seedlings grown in moist garden soil; *B*, in moist brown fibrous peat; *C*, in garden soil in which water level was maintained at approximately 2 cm. below soil surface; *D*, in brown fibrous peat in which water level was kept at about 2 cm. below soil surface; broken line shows location of soil surface, solid line of water surface; fig. 9, *Pinus Strobus;* fig. 10, *Abies balsamea;* fig. 11, *Picea excelsa.*

1. *Pinus Strobus* (fig. 9 *A*, *B*).—In both moist garden soil and moist peat the tap root assumed approximately the vertical position,

deviation from this direction being chiefly from the interference of the diagonal glass side of the growing box. It is also noteworthy that in both of these cases laterals were lacking. In garden soil in which a water table was kept, capillarity caused the water to rise until the soil was practically saturated to the surface. Only one pine seedling lived throughout this part of the experiment. A number of seedlings started to grow, however, and all behaved in the same way. All the tap roots showed a slight tendency to penetrate the soil, but the plants soon fell over and the roots grew in an approximately horizontal direction, producing no laterals (fig. 9 *C*). Those growing in peat in which a water level was kept behaved in a still different manner. On account of the fibrous spongy structure of the peat, aeration was possible to the water surface. The tap roots grew downward about as in the moist garden soil and peat, although somewhat less rapidly. The most obvious difference began to appear when the tips of the tap roots reached the water level, when growth almost completely ceased. In a few cases the roots continued to grow slowly for some time after reaching the water level, but in all cases these longer roots died back to about the surface of the water. Strong laterals always appeared and took approximately the horizontal position. The study of this species was suggested by the statement made by PULLING (7) that *Pinus Strobus* has "a deep rigid root habit." In examining the root systems of this tree at various ages in the Hillside bog and at Mineral Spring no root was found extending more than a few centimeters deep and all were horizontal. From this experiment and from field observation it is obvious that the tap root is ephemeral under bog conditions, and that very shallow horizontal laterals make up the entire root system.

2. *Abies balsamea* (fig. 10).—Under all the conditions of this experiment the roots grew downward and all were putting out laterals at the end of the experiment. At the water surface the roots behaved as in the case of *Pinus Strobus*.

3. *Picea excelsa* (fig. 11).—Throughout there was evident a decided tendency for the roots to assume an almost horizontal position. In some cases the roots penetrated somewhat below the water surface without showing any ill effects, although the rate of growth was greatly checked on entering the water.

Discussion

A comparison of the action of the roots of seedlings under experimental control with observations in the field shows that there are four general types of behavior of subterranean organs in these bogs.

1. The roots and rhizomes assume an approximately horizontal position above the water table. Typical forms are *Aspidium Thelypteris*, *Picea excelsa*, *Larix laricina* (fig. 2), *Carex filiformis*, *Pogonia ophioglossoides*, *Potentilla palustris*, *Lathyrus palustris*, and *Vaccinium macrocarpon*.

2. The tap roots of the seedlings die at the water surface and horizontal laterals appear above. Examples are *Pinus Strobus* and *Abies balsamea*.

3. All underground parts are approximately vertical and die near the water surface, usually with non-horizontal laterals or adventitious roots appearing above, as in *Sphagnum*, *Calopogon pulchellus*, *Sarracenia purpurea* (fig. 5), and *Drosera rotundifolia*.

4. The rhizomes and roots are able to grow under water. Important species are *Typha latifolia*, *Sagittaria latifolia*, *Scirpus validus*, *Eriophorum*, *Betula pumila*, and *Decodon verticillatus*.

While doubtless there are many factors influencing the location of roots and rhizomes in bog soils, it becomes evident that the two most potent are hereditary tendencies and water level. Rhizomes of certain plants, such as *Typha*, assume a depth apparently determined by heredity, which places them below the surface of the water. Such plants as can readily endure submergence are able to persist in the bog unless other factors interfere. Obligate deep-rooted plants which are intolerant of submergence are eliminated by water from this flora. Rhizomes of certain other species, as for example *Aspidium Thelypteris*, are in all cases superficial, thus permitting their development above water. On the other hand, the roots especially seem to respond rather readily to the water surface. A number of species have only shallow roots where the water table is high, but deeper ones in most peat or moist mineral soil. This was found to be especially well illustrated by *Aspidium Thelypteris*, *Pinus Strobus*, and *Acer rubrum;* hence it is apparently not the quality of the soil but the presence of water that induces shallowness. Doubtless the lack of oxygen plays a considerable part in checking growth under water. It is possible that bog toxins may in part be responsible for the poor development or in some cases even the death of the roots of certain species.

Summary

1. Subterranean systems of plants growing on floating mats were found to be very superficial, nearly all the living tissue being above the level of the water.

2. No evidence was found to suggest that acidity or toxins are involved in the shallowness of these organs. Water level was apparently the important factor, aside from hereditary tendencies in certain species.

3. Roots of codominants were in close competition without apparent damage resulting to them.

4. Three types of behavior were noted, resulting in the superficial placing of the living parts of bog plants: (*a*) the parts assume the horizontal position above the water level; (*b*) the tap root is ephemeral in the bog and is replaced by horizontal laterals; (*c*) the roots are all vertical and die at the water surface.

5. Certain plant parts were found to be able to thrive under the water in the bogs.

6. There is no apparent marked difference in the subterranean organs of a given species growing in a bog and in comparable conditions in mineral soils.

I wish to express my appreciation to Dr. H. C. Cowles and Dr. Geo. D. Fuller for encouragement and helpful suggestions during the progress of this work.

Penn College
Oskaloosa, Iowa

LITERATURE CITED

1. Cannon, W. A., The root habits of desert plants. Carn. Inst. Wash. Publ. 131. 1911.
2. ———, Notes on root variation in some desert plants. Plant World 16: 323–341. 1913.
3. Hayden, Ada, The ecological subterranean anatomy of some plants of a prairie province in central Iowa. Jour. Bot. 6:87–105. 1919.

4. HITCHCOCK, A. S., Studies on subterranean organs. Trans. Acad. Sci. St. Louis **9**: 1–8. 1899; **10**: 131–142. 1900.
5. HOPKINS, C. G., et al., Lake County soils. Univ. Ill. Agric. Exper. Sta. Soil Rept. no. 9. 1915.
6. MARKLE, M. S., Root systems of certain desert plants. BOT. GAZ. **64**: 177–205. 1917.
7. PULLING, H. E., Root habits and plant distribution in the far north. Plant World **21**: 223–233. 1918.
8. SHERFF, E. E., The vegetation of Skokie Marsh. BOT. GAZ. **52**: 415–435. 1912.
9. WEAVER, J. E., The ecological relations of roots. Carn. Inst. Wash. Publ. 286. 1919.
10. ———, Root development in the grass land formation. Carn. Inst. Wash. Publ. 292. 1920.
11. WHERRY, E. T., Soil acidity and a field method for its measurement. Ecology **1**: 160–173. 1920.
12. YAPP, R. H., Wicken Fen. New Phytol. **7**: 61–81. 1908.